



Spatial patterns and competition in trees in early successional reclaimed and natural boreal forests



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ABSTRACT

Spatial distribution of plants in early successional stands provides an indication of future plant community structure and population dynamics. Determining the factors driving plant interactions and their demographic relationships at stand initiation is critical to gain a better understanding of plants' responses to competition and limited resource conditions. Reclaimed ecosystems are ideal for studying such community mechanisms because they are completely reconstructed ecosystems with known community filters such as soil type, propagule composition, and the presence of both planted and naturally establishing trees. The current study explored the spatial patterns and competition-facilitation mechanisms in deciduous and evergreen trees in two oil sands reclaimed sites with different reclamation age (2-year old and 5-year old) and cover soils (wetland peat origin – PMM; and forest floor origin – FFMM) in Alberta, Canada, and compared this with a naturally-disturbed site at 5 years since fire. Spatial point pattern analysis was performed using pair correlation function $g(r)$, mark correlation function $k_{mm}(r)$, and bivariate g -function. Intraspecific competition in deciduous seedlings was stronger in the 5-year old reclaimed site than in the 2-year old site. Spatial patterns in deciduous seedlings on PMM were aggregated at 1–3 m scale similar to the natural site, whereas seedlings on FFMM sites had aggregated patterns at greater than 5 m scale. Planted conifers had regular pattern at 1–2 m scale in the 2-year old sites which reflects the plantation spacing, but showed a random pattern in the 5-year old sites indicating the effect of random mortality. Bivariate spatial analysis indicated a significant repulsion between deciduous and coniferous seedling at 1 m in the 2-year old PMM site and a significant attraction in the 5-year old FFMM site suggesting that the mechanism of competition-facilitation between trees is different in different cover soils. Density dependent thinning was only observed in the 2-year old PMM and natural sites; however, a gradual increase in nearest neighbour distances with increasing seedling size in all the reclaimed sites suggests that density dependent thinning has started.

1. Introduction

Competition is thought to be one of the key ecological mechanisms defining neighbourhood species distribution, survival and mortality, productivity, stand structure, population dynamics, and overall ecosystem function (Felinks and Wiegand, 2008; Getzin et al., 2006; Tilman, 1994). In boreal ecosystems, large scale disturbances (natural or anthropogenic) work in parallel with competition to shape the spatial pattern of vegetation (Felinks and Wiegand, 2008; Gray and He, 2009). As competition is a process mainly affecting neighbouring individuals, spatial locations of plants might reveal important information on community mechanisms directly related to competition such as dispersal, isolation, and density dependence (Gray and He, 2009; McIntire and Fajardo, 2009). Spatial patterns can also be used as an

indicator of vegetation succession since the distribution of one species may have influence on the surrounding species and the interplay among different species changes with time (Bertness and Callaway, 1994; Dale, 2000; Felinks and Wiegand, 2008). In natural ecosystems, most species show a systematic change in spatial patterns over time starting from random or aggregated and progressing to regular pattern due to competition driven either by density dependent mortality (He and Duncan, 2000; Newton and Jolliffe, 1998) or by the cumulative effects of competition and gap dynamics (Moeur, 1997). Disturbance generated heterogeneity in resource availability may also contribute to creating an aggregated pattern which can in turn be amplified or suppressed by biotic processes such as competition or facilitation (Miller et al., 2010).

Spatial patterns in naturally established plant communities are often a result of multiple complex processes working simultaneously, and

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disentangling the interplay between processes and emerging patterns may not always be possible due to our limited understanding of the intricate relationships among the contributing factors (Felinks and Wiegand, 2008; McIntire and Fajardo, 2009; Miller et al., 2010). Using fully stem mapped data, any small scale spatial correlation structure in the pattern of tree distribution can be quantified and the nature of their association (positive or negative) can be detected through spatial statistics such as Ripley's K-function and pair-correlation function (Ripley, 1976; Stoyan and Stoyan, 1994). For example, a positive association between two species at a certain scale may indicate a possible facilitation or mutual stimulation, whereas a negative association suggests repulsion and therefore interspecific competition (Callaway and Walker, 1997; Wiegand et al., 2007).

Studying spatial patterns of plant communities in reclaimed ecosystems has potential to answer some of these questions due to the controlled and known community filters such as soil type, propagule composition, and trackable early successional vegetation dynamics. Moreover, analysis of community structure and spatial distribution in the reclaimed areas may provide empirical evidence for improving reclamation techniques to achieve a target population structure. Although the aim of land reclamation and ecological restoration is to create conditions for natural ecosystem processes to operate, spatial patterns have rarely been considered as a key success attribute (SERI (Society for Ecological Restoration International Science & Policy Working Group), 2004).

Plant communities in reclaimed ecosystems may not display similar spatial patterns as in natural systems due to altered biotic (propagule availability, density dependence, soil microbial community, and herbivory) and abiotic (soil physical structure and chemical properties, microtopography, and environmental factors) conditions (Miller et al., 2010). Spatial patterns in reclaimed ecosystems may arise from several means such as distribution of cover soils, seed propagules transferred from the donor sites, naturally established seedlings from off-site sources, and planted species (Bakker, 2000; Rokich et al., 2000). Uniform sub-surface soil physical and chemical properties in reclaimed sites may also contribute to generate a uniform (at initial phase) to random (at maturity) vegetation pattern compared to the aggregated to random or regular pattern in natural systems (Milder et al., 2013; Miller et al., 2010; Silk et al., 2006). Spatial structures in plants during stand initiation greatly influences the density dependent interactions and structural complexity at later stages along the successional trajectory of stands (Donato et al., 2012; Swanson et al., 2011; Wild et al., 2014). These effects might be different in reclaimed and natural systems due to the differences in vegetation composition, mode of regeneration (seed origin vs sucker origin), and initial recruitment density, but are expected to change over time as the inter and intraspecific competition change as a result of density dependence (Johnson et al., 2012; Stachowicz, 2001). However, homogenization of substrates during the reconstruction of reclaimed sites may hinder the spatial structuring process for a long time (e.g. 100 years in an abandoned agricultural field (Flinn and Marks, 2007)). According to the resource heterogeneity hypothesis (RHH), the areas with homogeneous limited resource conditions may result in a patch-scale pattern that is less variable than the areas with spatially heterogeneous resource conditions (Tilman and Pacala, 1993). Although reclaimed ecosystems render an ideal opportunity to test such ecological hypothesis, there are actually very few studies that attempted to do so (Blignaut and Milton, 2005; Maestre et al., 2003; Miller et al., 2010; Valladares and Gianoli, 2007) and we are aware of only two studies conducted in oil sands reclaimed ecosystems but with heavy belowground components (Das Gupta et al., 2015; Sorenson et al., 2017).

In this study we explored spatial patterns in tree seedlings at an early stage of secondary succession on young oil sands reclaimed and post-fire sites in northern Alberta, Canada. We quantified spatial structures in both planted and naturally regenerating tree seedlings on sites reclaimed at two different ages with two different cover soils and

compared this with a natural fire disturbed benchmark site. We asked the following questions: (1) What spatial patterns do seedlings show in different reclaimed and naturally-disturbed sites? Spatial patterns in seedlings should be different in reclaimed and naturally-disturbed sites due to the differences in population dynamics (e.g. recruitment density and regeneration mode) and abiotic conditions. (2) Are the competitive forces (intra- and interspecific) different in the reclaimed and naturally-disturbed sites? Importance of interspecific competition should be stronger (high r^2 between seedling size and neighbourhood distance) in the reclaimed sites than the naturally-disturbed site due to the competition for limited resources in the reclaimed sites. (3) Is there any evidence of density dependent competition between seedlings of different size classes in the reclaimed and naturally-disturbed sites? We expected to see a clear evidence of density dependent thinning in sites with high seedling density. A gradual decline in clustering and increase in neighbourhood distances with increasing seedling size may indicate density dependent thinning (Getzin et al., 2008b).

2. Methods

2.1. Site description

This study was conducted in 2015 at an oil sands mine 75 km north of Fort McMurray, Alberta, Canada (57° 20' N, 111° 49' W). The natural forest ecosystem in the region is boreal mixedwood forest with the mesic upland sites consisting of varying mixtures of deciduous (mainly trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*)) and coniferous (mainly white spruce (*Picea glauca*)) trees. The dominant soil type is well drained Orthic Gray Luvisol (Beckingham and Archibald, 1996). The continental climate has a mean July temperature of 16.8 °C and January temperature of – 18.8 °C with mean annual precipitation of 455 mm (Environment Canada, 2016).

Two young reclaimed sites, a 2-year old and a 5-year old site, were used in the current study. The reclaimed sites were overburden dumps constructed of saline – sodic overburden material produced during oil sands mining and subsequent reclamation in 2013 and 2011, respectively. The overburden material was covered with 1 m of suitable (i.e. non-saline) sub-soil and then 0.2–0.5 m of reclamation cover soil was directly placed. Two types of reclamation cover soils were used in the study: (i) peat – mineral mix (PMM) derived from wetland peat deposits and underlying mineral soils, and (ii) forest floor – mineral mix (FFMM) derived from upland forest soil created by salvaging the forest floor layer and underlying mineral soils together. A 5-year old post-fire stand was used as natural benchmark since fire is the main natural disturbance and one of the main drivers of the spatial community processes in the studied boreal region (Nilsson and Wardle, 2005; Payette et al., 2008). Sampling was done in 2015. All the sites were located within a 10 km radius of each other and experienced similar weather conditions and propagule pressure. The deciduous trees in the studied plots were of natural origin and comprised of trembling aspen (70–90% of the total stems) and balsam poplar (15–23% of total stems), whereas white spruce (3–30% of total stems) was the only conifer that was planted on the reclaimed sites at a density of approximately 1900 stems per hectare (Table 1). Plantation is a part of the standard reclamation practice in the oil sands mining areas. Conifer seedlings were nursery grown and 1-year old when they were planted in the reclaimed sites (5-year old in 2015). The deciduous trees on the reclaimed sites are of seedling origin while on the natural site they are of sucker origin (only trembling aspen). The term seedling will be used to refer to all trees regardless of origin: seedling, sucker, planted. The general soil and site characteristics of the studied area can be found in (Pinno and Errington, 2015). In general, PMM soils were more acidic and had lower bulk density and greater N and S than the FFMM and benchmark soils (SI: Table S1).

Table 1
Density (ha^{-1}) and nearest neighbour distance (m) of trees in the studied reclaimed and naturally-disturbed wildfire sites in northern Alberta.

Site	2-year old reclaimed			5-year old reclaimed			5-year old post-fire	
	< NN_{dist} >	Deciduous	Coniferous	< NN_{dist} >	Deciduous	Coniferous	< NN_{dist} >	Deciduous
PMM	0.90	17,400	1866	0.46	89,600	1900	0.60	51,900
FFMM	1.57	4650	1900	0.78	31,100	3400		

< > = mean; NNdist = nearest neighbour distance.

2.2. Stem mapping

A total of five plots were used for stem mapping and measurements; two plots in each reclaimed site (FFMM and PMM in each) and one plot in the wildfire site. Plots were selected based on a density of at least 4000 deciduous seedlings per hectare due to the variable recruitment in different cover soil types. A 200 m^2 ($20 \text{ m} \times 10 \text{ m}$) plot was used in the 5-year old and natural benchmark sites. A larger plot ($20 \text{ m} \times 15 \text{ m}$) was used in the 2-year old sites to account for the lower seedling density. Previous studies showed that the recruitment and spatial dynamics in aspen seedlings were more dependent on fine scale (few meters) site attributes rather than the coarse scale features (Namroud et al., 2005; Turner et al., 2003). In reclaimed sites, spatial distribution of aspen and coniferous seedlings showed detectable patterns at even less than 2 m scale (Sorenson et al., 2017). The selected plot sizes are therefore appropriate to capture the spatial dynamics in the studied seedlings. In each plot, all the seedlings with $\geq 1.0 \text{ mm}$ bole diameter were mapped, their top heights were recorded, and stems were identified to species.

2.3. Data analysis

2.3.1. Spatial pattern

Pair correlation function (PCF) $g(r)$ (Stoyan and Stoyan, 1994) was used to quantify the spatial structure of the uni- and bivariate patterns in seedlings (research question 1). Pair correlation function is a point-to-point distance function that describes aggregation and regularity at a certain radius r (Wiegand and Moloney, 2004). Univariate pair correlation function can be defined from the neighbourhood density function $O_{11}(r) = \lambda_1 g_{11}(r)$, where O_{11} is the mean density of species 1 within a ring with radius r , and λ is the intensity i.e. number of individual in the plot/area of the plot (Wiegand and Moloney, 2004). Likewise, bivariate pair-correlation function $g_{12}(r)$ can be derived from bivariate neighbourhood density function $O_{12}(r) = \lambda_2 g_{12}(r)$, which is the ratio of the observed mean density of species 2 within the distance r of arbitrary species 1 to the expected mean density of species 2 within the ring with radius r . Under complete spatial randomness (CSR) $g(r) = 1$, $g(r) > 1$ indicates aggregation (patchy pattern), and $g(r) < 1$ indicates regularity.

We tested the observed spatial pattern in individuals against the null model of homogenous Poisson process for departure from complete spatial randomness (CSR), and inhomogeneous PCF with an inhomogeneous Poisson null model to account for any possible large scale environmental heterogeneity. The inhomogeneous Poisson null model allows to detect significant plant-plant interactions (second order effects) after factoring out the potential environmental heterogeneity (first order effect) within a given local neighbourhood of radius h (Stoyan and Stoyan, 1994). Therefore, any spatial structures at scale smaller than h are removed from the pattern. A non-parametric estimates of the intensity function based on the Epanechnikov kernel (Wiegand and Moloney, 2004) was used with a bandwidth of 5 m. Both null models were applied to all individuals in all the plots. Departure from a given null model was tested by comparing the pair correlation function of point data with the 5th lowest and 5th highest value of 199 Monte Carlo simulation to generate an approximately 95% simulation envelope. Thus, a $g_{11}(r)$ above the simulation envelope in the univariate

analysis indicates clustering, whereas below the envelope indicates regularity. In bivariate analysis, observed $g_{12}(r)$ above the simulation envelope indicates positive association i.e. attraction and below the envelope suggests negative association i.e. repulsion. Edge correction was done according to Wiegand and Moloney (2004). A goodness of fit (GoF) test (Loosmore and Ford, 2006) was used to avoid spurious rejection of null model and to determine the level of significance of the function output at certain distances of interest (in this case 0–5 m). Deviations from the null model were considered significant if the p value from the goodness of fit test was smaller than 0.05. All point pattern analyses were conducted using *Programita* software (Wiegand and Moloney, 2004) and Spatstat library (Baddeley and Turner, 2005) in R.

2.3.2. Relative importance of competition and growth impact

The relative importance of competition between tree seedlings (research question 2) was analysed using the relationship between seedling size and their nearest neighbour distances (Shackleton, 2002). A size-distance correlation was determined between the sum of the bole diameters of the nearest 5 seedlings of a focal seedling plus the bole diameter of the focal seedling and the sum of the distances of the nearest 5 neighbours. The coefficient of determination (r^2) of the relationship has been shown to be a robust index of relative importance of competition among trees (Welden et al., 1988). We classified the size-distance relationship into two categories: interspecific competition (focal seedlings with heterospecific neighbours) and intraspecific competition (focal seedling with conspecific neighbours). Importance of inter- and intra-specific competition was measured by the r^2 from the size-distance relationship.

Effect of intra and interspecific competition on seedling growth was analysed using both univariate and bivariate mark correlation function $k_{mm}(r)$ (Getzin et al., 2008a; Stoyan and Stoyan, 1994). Seedling bole diameter was used as a mark to identify distance dependent size correlation of seedlings. Similarity between bole diameter of two seedlings at a distance r apart can be quantified using the test function of the normalized mark correlation function $(k_{mm})f(m_1, m_2) = m_1 \times m_2$, where m_1 and m_2 are the bole diameter of two neighbouring seedlings. Similarly, bivariate mark correlation function quantifies the relationship between the size of a focal tree to the size of individuals of all other species that are located distance r from the focal tree. Values of k_{mm} larger or smaller than 1 indicate individuals tend to have larger or smaller mark (bole diameter in this case) values than the plot mean, i.e. mutual stimulation (positive correlation) or inhibition (negative correlation). Departure from the null model of independent bole diameter distribution was quantified using a 95% confidence interval of 199 Monte Carlo simulations using random labelling which shuffled the measured bole diameter among all the stems but kept the stem position fixed. The null hypothesis assumes that the bole diameter values are independent of the spatial position of individuals (Stoyan and Stoyan, 1994).

2.3.3. Density-dependent thinning

Density dependent thinning is a commonly observed competition mechanism in plant community and found in every size classes starting from very small seedlings to large adults (Moer, 1997). Here we estimated the effect of density dependent thinning on the spatial

distribution of deciduous seedlings of different size classes in reclaimed and natural sites (research question 3). The signature of density dependent thinning was analysed using qualitative random labelling with a case control design of different size classes. We used four size classes for seedling bole diameter: very small seedling 0–5 mm, small seedling 5–10 mm, medium seedling 10–15 mm, and large seedling > 15 mm bole diameter. The large seedling class was only found in the natural benchmark site. Very small and small seedling classes were merged in the natural site to avoid inverse density effect as few seedlings fell in the very small seedling size class. We compared the spatial pattern of smaller seedlings with that of large seedlings (control) assuming that the larger seedlings reflect underlying environmental and resource heterogeneity (Getzin et al., 2008b). A gradual decline in aggregation with increasing size can be considered as the result of density dependent thinning and the strength of this decline relative to control indicates the magnitude of density dependent thinning (Getzin et al., 2008b).

Case control random labelling was performed using the bivariate g -function (Getzin et al., 2006). Under random thinning, the g -function is invariant of size classes i.e. $g_{12}(r) = g_{21}(r) = g_{11}(r) = g_{22}(r)$. Departure from bivariate random labelling was assessed using the $g_{12}(r)-g_{11}(r)$ and $g_{22}(r)-g_{21}(r)$ test statistics. Test statistic $g_{12}(r)-g_{11}(r)$ reveals if small and large seedlings have similar spatial patterns and $g_{22}(r)-g_{21}(r)$ tests whether there is an additional clustering within smaller seedlings independent from the distribution of large seedlings (Getzin et al., 2006; Watson et al., 2007).

3. Results

3.1. Vegetation composition and structure

The mean nearest neighbour distance among seedlings was smaller in the 5-year old reclaimed sites than the 2-year old sites, while among reclamation soil types the highest deciduous seedling density was found in the PMM sites which also had smaller nearest neighbour distances than the FFMM sites (Table 1). The 5-year old PMM site had a comparable deciduous density and nearest neighbour distance pattern similar to the natural site (Table 1). Deciduous seedlings had similar bole diameter distribution in the reclaimed and natural sites, but the natural site had more large seedlings (Fig. 1).

3.2. Spatial patterns

Inhomogeneous PCF was used in all the plots to determine the presence of any potential large-scale environmental heterogeneity; however, no significant large scale departure from CSR was detected indicating environmental homogeneity within the plots. Therefore, only homogeneous PCF was used for all the subsequent spatial analyses. Deciduous seedlings on the 2-year old sites had an aggregated pattern (GoF $p \leq 0.05$) at 1–1.5 m scale in PMM, and at 1–5 m scale in FFMM (Fig. 2a, c). In the 5-year old sites, the scale of clustering changed to 1–3 m in PMM site but remained the same 1–5 m in the FFMM site (Fig. 2e, g). Deciduous seedlings were aggregated at 1 m scale in the natural site (Fig. 2i). Planted conifers showed a regular pattern (GoF $p \leq 0.05$) at ~ 2 m scale in both 2-year old PMM and FFMM sites (Fig. 2b, d) but were mostly randomly distributed in the 5-year old sites (Fig. 2f, h).

The bivariate patterns of spatial association between deciduous and coniferous seedlings in the reclaimed sites showed both attraction and repulsion. In the 2-year old PMM site, a significant negative association (GoF $p \leq 0.05$) at 1 m scale indicates repulsion between the deciduous and coniferous seedlings (Fig. 3a). However, no significant association was detected in the 2-year old FFMM site. Deciduous and coniferous seedlings on the 5-year old FFMM site, on the other hand, showed a significant positive association (GoF $p \leq 0.05$) at 1–1.5 m scale indicating a significant attraction (Fig. 3d), while the 5-year old PMM site

also did not show any significant associations.

3.3. Competition and growth impacts

The importance of intraspecific competition in deciduous trees is stronger on FFMM than PMM and stronger in the 5-year old sites than the 2-year old sites (Fig. 4). The importance of interspecific competition from conifers did not vary among soil types or stand ages. There were not enough conifer seedlings within the neighbourhood to calculate the importance of intraspecific competition in conifers. Mark correlation analysis did not detect any significant growth impact (suppression or stimulation) on seedling bole diameters (data not shown).

3.4. Inference on density dependent thinning

The effect of density dependent thinning (scale and strength) on the distribution of the deciduous seedlings of different size classes was compared between reclaimed and natural sites. The random labelling analysis showed that on the 2-year old PMM site the small seedlings were clustered (GoF $p \leq 0.05$) around the large seedlings at a scale of 0.5 m–3 m (Fig. 5a and b; inset). The distribution of the smallest seedlings around themselves differed significantly (GoF $p \leq 0.05$) from random labelling at all distances from 1 to 5 m scale indicating very strong clustering ($g_{21}(r) - g_{22}(r)$; Fig. 5a). The significant clustering disappeared for the next size class (small seedlings) indicating the effect of density dependent thinning (Fig. 5b). The distribution of small seedlings in the 2-year old FFMM site followed a similar overall pattern of the large seedlings with no significant departure from random labelling (Fig. 5c).

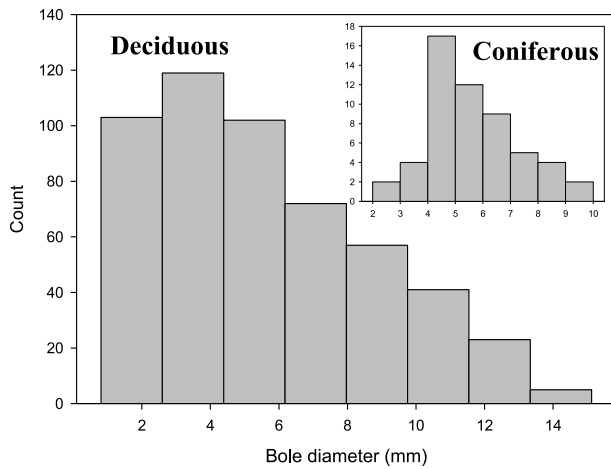
Small seedlings on the 5-year old PMM site showed an additional clustering different from the pattern of large seedlings ($g_{12}(r) - g_{11}(r)$; Fig. 5d and e inset); however, no significant seedling to seedling clustering was detected ($g_{21}(r) - g_{22}(r)$; Fig. 5d and e). The test statistic $g_{12}(r) - g_{11}(r)$ and $g_{21}(r) - g_{22}(r)$ did not differ significantly from the random labelling for the seedlings on the 5-year old FFMM site (Fig. 5f) suggesting a homogeneous spatial distribution between small and large seedlings.

In the natural site, the distribution of small and medium seedlings around the large seedlings followed similar patterns ($g_{12}(r) - g_{11}(r)$; Fig. 5g and h inset). However, strong clustering (GoF $p \leq 0.05$) was found only for the small seedlings at a scale of 1–2 m ($g_{21}(r) - g_{22}(r)$; Fig. 5g). The clustering disappeared for medium sized seedlings which again confirm the evidence of density dependent thinning (Fig. 5h). Moreover, a gradual increase in seedling size (bole diameter) with increasing nearest neighbour distance was also observed in all the sites (Table 2).

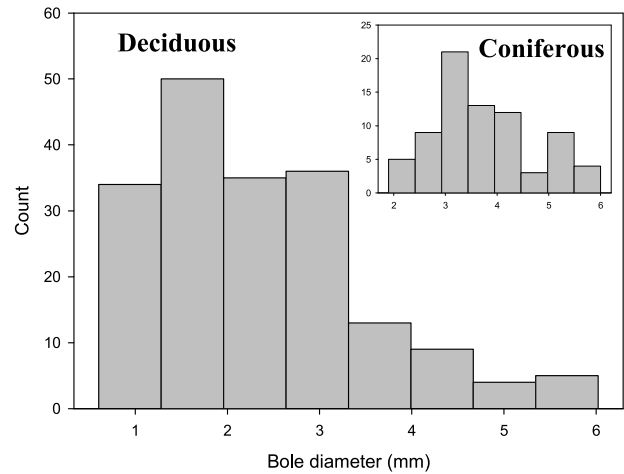
4. Discussion

The main objective of this study was to characterize spatial patterns of trees and their competitive behaviours in young oil sands reclamation sites compared to a naturally-disturbed benchmark site. The current study also highlights the importance of belowground substrates and resource conditions in spatial patterning of seedlings at stand initiation and proposed a number of key competition-facilitation mechanisms at play. The detailed spatial analyses clearly shows that intra- and inter-specific forces driving the plant community dynamics are non-random. For example, deciduous seedlings on both reclaimed and natural sites showed aggregated pattern at different spatial scales, whereas coniferous seedlings had both regular and random patterns. The stronger intraspecific competition in deciduous seedling in the 5-year old reclaimed sites compared to the 2-year old sites indicates that intraspecific competition is one of the key drivers of spatial distribution and population dynamics of deciduous trees in these sites. In natural systems, such a mechanism of spatial patterning is confirmed by several studies (Fangliang et al., 1997; Felinks and Wiegand, 2008; Gray and

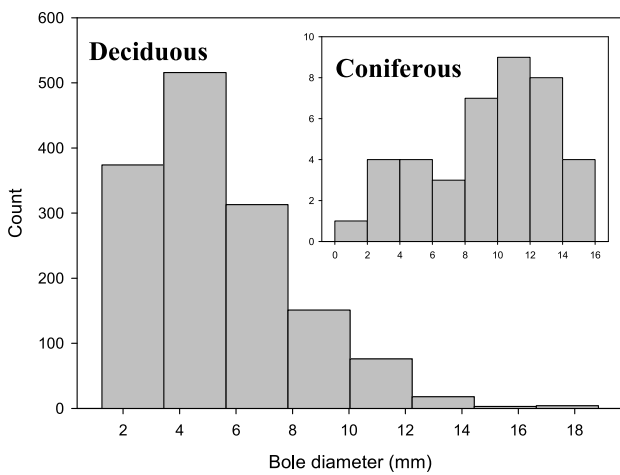
(a) 2-year old PMM



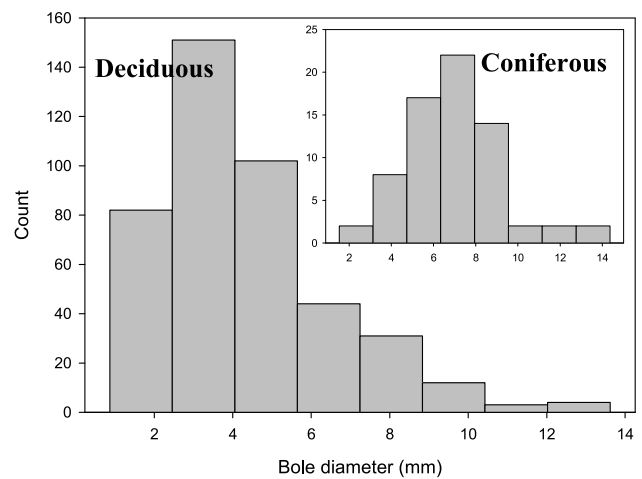
(b) 2-year old FFMM



(c) 5-year old PMM



(d) 5-year old FFMM



(e) 5-year old post-fire

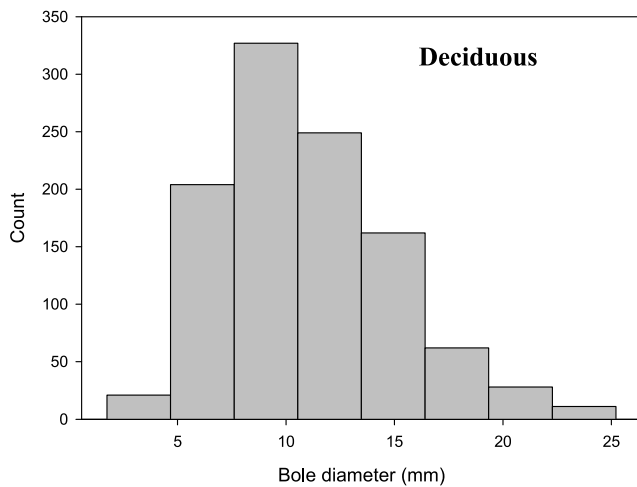


Fig. 1. Distribution of bole diameter of deciduous and coniferous (inset) seedlings in oil sands reclaimed and naturally-disturbed post-fire sites in northern Alberta.

He, 2009; Szwagrzyk and Czerwczak, 1993). Miller et al. (2010), however, demonstrated the importance of dispersal limitation and abiotic processes along with the competitive interactions in structuring the spatial distribution of vegetation in restored shrublands. Regular

spatial pattern in coniferous seedlings at 2 m scale reflected the spacing used during plantation, but the random pattern in the 5-year old sites indicates random mortality which might have resulted from the inter-specific competition from the deciduous seedling and other understory

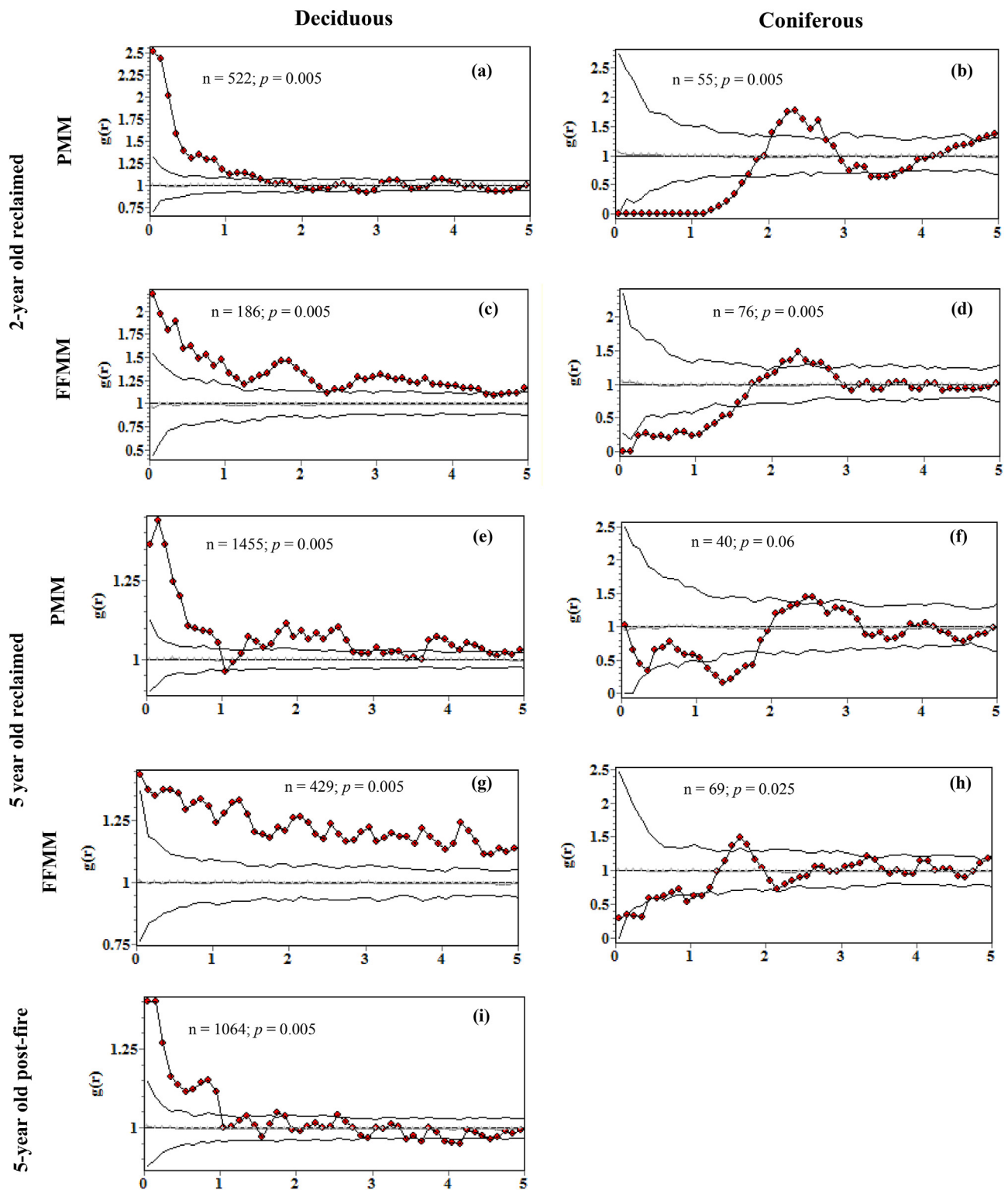


Fig. 2. Univariate patterns of deciduous and coniferous seedlings in oil sands reclaimed and post-fire sites in northern Alberta analysed using $g(r)$ and complete spatial randomness (CSR) null model. $g(r)$ = black solid line with red diamonds; 95% upper and lower confidence limit = gray lines. No conifer seedling was found in the natural site. P corresponds to the goodness-of-fit test (Loosmore and Ford, 2006) and n is number of individuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

vegetation.

We expected to see different spatial patterns in naturally regenerating seedlings on the reclaimed and benchmark sites due to the differences in biophysical attributes such as substrate quality, nutrient supply rate, and microhabitat conditions (see Pinno and Errington,

2015). Deciduous seedlings on FFMM sites had an aggregated pattern at scales different than the natural site (5 m vs 1 m), but seedlings on PMM sites had similar patterns (1.5 m vs 1 m). Development of spatial structure is a result of multi-generation feedback processes and might not be detectable unless the driving forces (competition or facilitation,

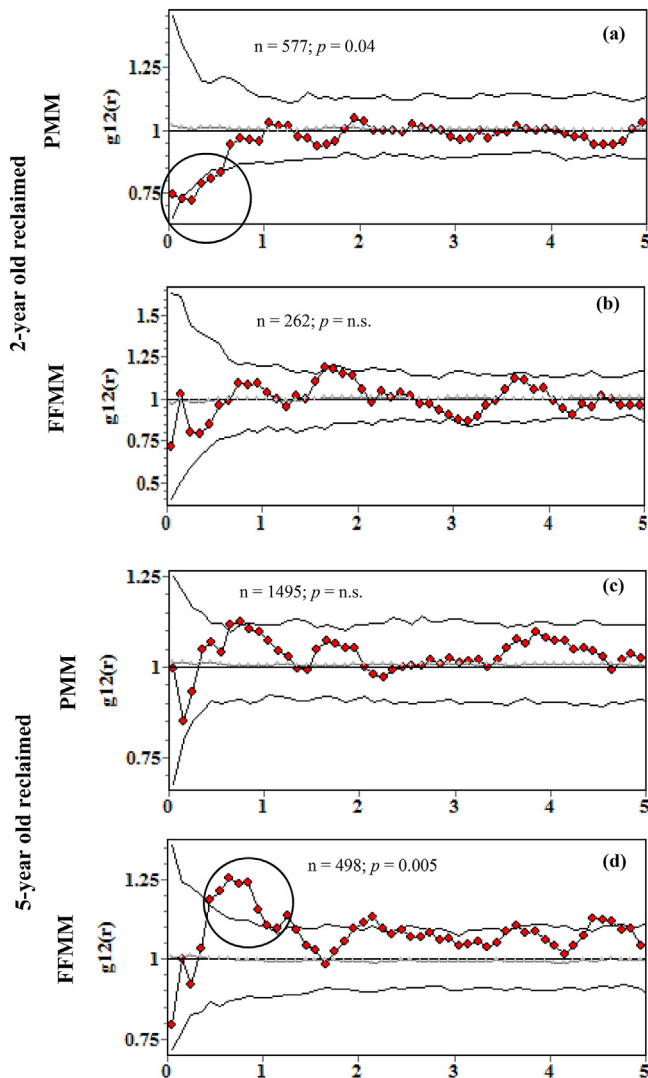


Fig. 3. Bivariate analysis with pair correlation function (g -function) showing spatial associations between deciduous and coniferous species in different oil sands reclaimed sites in northern Alberta. Complete spatial randomness was used as null model. $g(r)$ = black solid line; 95% upper and lower confidence limit = gray lines. Significant attraction and repulsion indicated by the black circle. P corresponds to the goodness-of-fit test (Loosmore and Ford, 2006) and n is number of individuals; n.s. = Not significant.

resource heterogeneity, and environmental factors) are strong enough to create a pattern (Miller et al., 2010; Stoll and Bergius, 2005). The reclamation sites might therefore suffer from low resource heterogeneity (Nyamadzawo et al., 2008; Shukla et al., 2007), seedling recruitment (Elmarsdottir et al., 2003; González-Alday et al., 2009; Holl, 2002; Mackenzie and Naeth, 2007), and seedling density (Pinno and Errington, 2015) at initiation to create a spatial pattern similar to that in naturally-disturbed systems. These limitations will also vary between different cover soil treatments used for reclamation. The observed differences in the spatial structure between PMM and FFMM is likely due to the differences in belowground properties. The cover soils used in the FFMM sites are full of seed propagules from the upland donor sites (Mackenzie and Naeth, 2007, 2010). Thus, naturally regenerating seedlings experience a higher competitive pressure in these sites than in the PMM sites resulting in lower tree establishment densities. The similar scale of aggregation and mean nearest neighbour distance in the PMM and post-fire sites could mainly be attributed to the high seedling density in these sites. Seedling recruitment density is often an indication of establishment limitation and site productivity (Chen et al.,

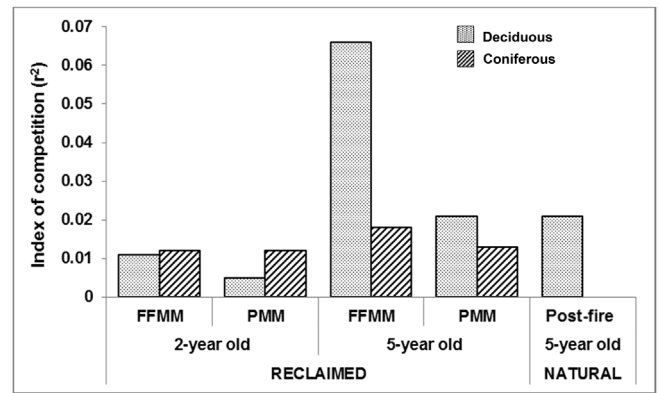


Fig. 4. Relative importance of competition in seedlings on oil sands reclaimed and post-fire sites in northern Alberta expressed as the correlation between seedling size and distance. Changes in the strength of relationship (r^2) between bole diameter and distances indicate either an increase or decrease in the relative importance of competition.

2013). Although the regeneration techniques of the deciduous seedlings were different in reclaimed (seed origin) and natural (sucker origin) sites, their high establishment success in these sites contributed greatly to the generated spatial patterns. The site level drivers of spatial distribution in seedlings can, however, be very different in reclaimed and natural sites. In post-fire sites, this could well be related to the distribution of the clonal parents and exposed mineral soils (Schier, 1975; Turner et al., 2003), whereas microsite conditions such as surface roughness, moisture gradient, and substrate quality (e.g. percent organic C) are likely to be more important in the reclaimed sites (Errington and Pinno, 2016; Pinno and Errington, 2015).

Both facilitation and competition are likely occurring between seedlings of different species in the reclaimed sites. The small scale bivariate attraction between deciduous and coniferous seedlings in the 5-year old FFMM site suggests interspecific facilitation. Facilitation may appear as a key mechanism of plant coexistence where abiotic stress (e.g. temperature, moisture and wind) or biotic stress from consumers (e.g. disturbance) is high (Bertness and Callaway, 1994). The importance of competition increases where the stress from physical environment is benign and consumer pressure is relatively low (Callaway, 1995; Callaway and Walker, 1997; Maestre et al., 2009). Aspen and balsam poplars are known to be heavily dependent on soil moisture availability for their germination and growth (Fechner et al., 1981; Wolken et al., 2010). So, the relatively low moisture availability and high competition in FFMM sites (Pinno and Errington, 2015) may have forced the facilitative interactions between seedlings. Hydraulic lift and microhabitat amelioration (e.g. shading from larger seedlings) are the two possible mechanisms that could be in play to favour this facilitation in FFMM. Hydraulic lift and redistribution have been shown to be important mechanisms for facilitative interactions between woody plants in moisture limited conditions (Quijano et al., 2012; Yu and D'Odorico, 2015). Similar stress dependent facilitation among tree seedlings was also demonstrated by Calder and St Clair (2012) in meadow-forest ecotone, Fajardo and McIntire (2011) in forest-prairie ecotone, Eränen and Kozlov (2008) in subarctic stress gradients, and among woody shrubs by many other studies in alpine and grassland ecosystems (see Maestre et al., 2009). PMM sites, on the other hand, are experiencing much higher moisture conditions leading to higher seedling recruitment and seedling densities (Pinno and Errington, 2015) and therefore the putative competitive force is much stronger than the facilitative force.

Thinning due to density-dependent competition is a spatial patterning mechanism which seems to have started in the reclaimed sites. The gradual disappearance of clustering and an increase in the mean neighbourhood distance with increasing seedling size are indicative of processes driven by density dependent interactions (Getzin et al.,

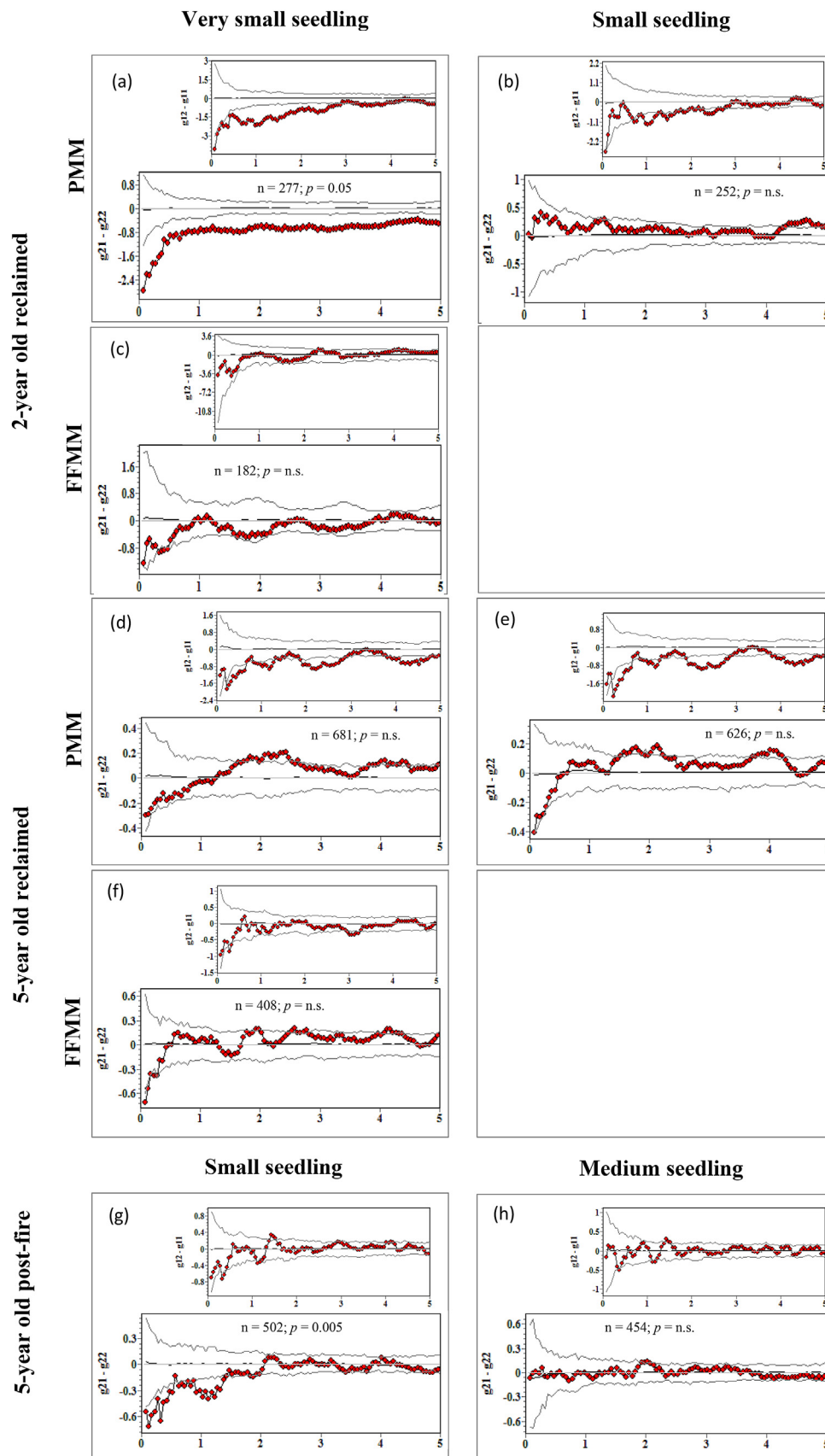


Fig. 5. Case control analysis (random labelling) of deciduous seedlings in different oil sands reclaimed and post-fire sites in northern Alberta. Pattern of large seedlings were used as control. The statistic $g_{12}(r) - g_{11}(r)$ tests if the specific size classes (very small, small and medium; pattern 2) follow the pattern of large seedlings (pattern 1). The statistic $g_{21}(r) - g_{22}(r)$ evaluates if seedlings are clustered due to a process independent from the pattern of large seedlings. P corresponds to the goodness-of-fit test (Loosmore and Ford, 2006) and n is number of individuals; n.s. = Not significant.

Table 2

Different size classes of deciduous seedling and their nearest neighbour distances in reclaimed and naturally-disturbed wildfire sites in northern Alberta.

	2-year old reclaimed						5-year old reclaimed						5-year old post-fire ^a		
	PMM			FFMM			PMM			FFMM			n	< dia. >	< dist. >
	n	< dia. >	< dist. >	n	< dia. >	< dist. >	n	< dia. >	< dist. >	n	< dia. >	< dist. >			
Very small seedling (dia. 0–5 mm)	219	2.96	1.34	164	2.11	1.86	628	3.47	0.66	296	3.23	0.96	361	7.63	0.89
Small seedling (dia. 5–10 mm)	194	7.16	1.46	18	4.83	6.35	573	7.13	0.73	112	7.23	1.58			
Medium seedling (dia. 10–15 mm)	58	11.66	2.37	–	–	–	53	12.75	2.28	–	–	–	313	12.08	1.00
Large seedling (dia. > 15 mm)	–												141	17.4	1.59

< > = mean; dia. = Bole diameter (mm); dist. = Nearest neighbour distance (m).

^a Very small and small seedling classes were combined in the fire site to avoid inverse density effect on the nearest neighbour distance as there were only few seedlings in the very small class.

2008b). We found a direct indication of density dependent thinning in the 2-year old PMM and natural sites from the case control analysis, and indirect evidence supported by the increasing neighbourhood distances with increasing seedling size in all the sites including FFMM. Although the case control analysis in the 5-year old PMM site failed to detect clustering in the smaller seedlings, this does not mean an absence of density dependent competition (Welden et al., 1988). Under highly dense conditions as such found on PMM, seedling recruitment to the next higher size classes may not be affected in the case of weak density dependent competition, and if the effect has already been reflected in the distribution of smaller sized seedlings (Getzin et al., 2008b). The possibility of such interference has been well documented in different ecosystems recovering from disturbances by Callaway (1995). In old growth forest, He & Duncan (He and Duncan, 2000), and Getzin et al. (2008b), found clear evidence of density dependent thinning supported by the gradual disappearance of clustering in large seedling and sapling classes. The absence of clustering in the small seedlings on FFMM could largely be attributed to the low seedling density. The current findings suggest that the competitive force driving density dependent thinning in the PMM and FFMM sites is different. Despite the absence of clustering in the smaller sized seedlings, the gradual increase in mean neighbourhood distances in all the reclaimed sites confirms that density dependent thinning has started and is playing a key role in defining intra and interspecific competition.

In conclusion, this study emphasized that spatial point patterns can be used in tracking and interpreting plant community dynamics in reclaimed sites. Although conifer seedlings were not present in the natural site, they were part of the reclaimed system and contributed to the overall spatial structure of other seedlings. We found an indication of strong intraspecific competition in deciduous seedlings in the older reclaimed sites which seems to be higher on FFMM than PMM. Despite having totally different soils and disturbance history, relatively similar spatial patterns in PMM and natural benchmark sites suggest that the early successional plant dynamics are following a similar trajectory of recovery. The low density of deciduous seedling and different spatial patterns in the FFMM sites raise a concern about the future stocking and spatial structure of trees in these reclaimed sites. Planting deciduous trees at high density or in cluster patches with variable species ratio in these sites might be an option to jumpstart the spatial structuring process.

Author contributions

Both authors contributed equally to this study. SDG and BDP conceived the idea and designed the study. SDG conducted fieldwork and performed data analysis. Both authors wrote the manuscript, provided editorial advice and approved the final version of the manuscript.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2018.05.003>.

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